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THE FUNCTION OF SABER-LIKE CANINES IN CARNIVOROUS MAMMALS

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INTRODUCTION

The development of saber-like upper canines in flesh-eating mammals has occurred independently at least three times, in the South American Pliocene marsupial *Thylacosmilus* (see Riggs, 1934), in the North American Eocene creodont *Apataelurus* (see Scott, 1938), and in the widespread Oligocene to Pleistocene machairodont cats. The machairodonts, at least, survived for millions of years and evidently found this structure eminently useful, but no living carnivore has anything of the sort. The bizarre and savage appearance of these teeth stimulates lay and scientific interest and invites speculation as to their function. The absence of any close recent analogy makes inferences difficult. It is not surprising that a large literature has grown up on the subject and that strong differences of opinion exist.

Nearly ninety years ago, Warren (1853) gave an excellent functional description of the canines and associated structures in *Smilodon*. He concluded that the canines transfix the prey and then cut and tore by movement of the head backwards. He thus foreshadowed both of the views variously emphasized by most later authors: that the canines were used for stabbing (transfixing) and for slicing (cutting and tearing). The stabbing theory was more explicitly developed by Brandes (1900), whose arguments were, however, weakened by the suggestion of adaptation for preying on glyptodonts. Of course, the fact is that the armor of the glyptodonts and the canines of the machairodonts were fully developed millions of years before these two sorts of animals ever came in contact with each other. Matthew (1901) suggested the most widely accepted theory: that the

usual prey was the thick-skinned ungulates, the action being to strike and then rip or gash so that the prey bled to death. This view was again and more fully developed in his later paper (Matthew, 1910), which is the classic and still the most useful treatment of this subject. Many later authors, for instance, Scott and Jepsen (1936), have emphasized stabbing or snake-like striking as the only or at least the most important function.

The most recent study is that of Bohlin (1940) who rejects the stabbing theory entirely and maintains that the sabers were ill-adapted for this function and must have served mainly or wholly for slicing. He concludes that the machairodonts were not predaceous but were primarily carrion-feeders, an idea previously suggested by Weber (1904), Marinelli (1938), and a few others, although the great majority of students have believed that all these saber-toothed flesh-eaters were eminently predatory.

Bohlin's study is so able and reasonable, despite its unusual conclusion, that it seemed at first reading to be definitive and to require radical revision of current ideas of sabertooth habits and history. It was, however, then noticed that certain of the arguments advanced by Bohlin as conclusively opposed to the stabbing theory apply with equal force to many of the front-fanged venomous snakes and could be used to "prove" that they cannot strike a stabbing blow or that their fangs are not adapted to this function, which is absurd. Evidently there is a fallacy either in Bohlin's arguments or in the analogy with these snakes, and reconsideration is necessary.

The snake analogy is imperfect and must

be carefully limited. The primary purpose of insertion of venomous snake fangs is different from that of the mammalian sabers, which certainly did not inject poison. The associated musculature and osteology are also very different in snakes. Some snakes do, however, insert the fangs by an efficient stabbing action and these fangs are usually, if not always, definitely more curved than they should be if Bohlin's argument is correct, and they are frequently inserted at a "wrong" angle. To this extent the analogy is valid. Relatively little detailed study seems to have been made of the exact motion of snake fangs in penetrating the prey. The best that I have seen (kindly brought to my attention by C. M. Bogert) is by Klauber (1939) and refers to rattlesnakes, the fangs of which are less analogous to mammalian saberteeth than are those of some of the other pit-vipers (e.g., *Bothrops*) and many of the elapids. Consideration of all these reptiles yields a vital clue: the fangs are driven in with a rotary movement and the mechanical center of this rotation does not necessarily or usually coincide with an anatomical joint.

Experiments were made with the skulls (originals or casts) of numerous machairodont cats and of *Thylacosmilus*. (The skull and sabers are unknown in *Apataelurus* although the presence of the latter is certain from the structure of the lower jaw.) These were supplemented by the manipulation of cut-outs and the study of successive tracings made as these were moved in various ways. The general anatomy of *Smilodon* (see especially Merriam and Stock, 1932) was also considered, along with the special features of musculature distinguishing it from the felines (especially Matthew, 1910, and Marinelli, 1938). Some of the results of this study are summarized in the following paragraphs.

Fundamental considerations are the mechanical nature of the canine and the points most conveniently used to represent and analyze motion of the head, in which the canines are immovably fixed. The axis of the canine may be taken as a curved, longitudinal line approximately in the center transversely (labiolingually) and at or near the part of the tooth that is thickest

transversely. This thickest part is seldom at the center of the tooth anteroposteriorly but usually more anterior. In *Thylacosmilus* it is marked by a definite ridge, on the labial side, but in the machairodonts the lingual and labial canine surfaces are smoothly curved. In most cases it is noticeable that this axis is more nearly parallel to the anterior than to the posterior margins of the tooth, especially in the more proximal part. The posterior margin is invariably formed by a more acute angle than the anterior and it bears a sharp cutting edge nearly or quite to the alveolus. Although more obtuse, the anterior margin is also always trenchant at least in its distal portion. A variable extent of the proximal part of this margin is usually rounded and not trenchant.

The points used to analyze head motion are (a) the tip of the canine, which leads the work, (b) the occipital condyles (or the projection of a transverse axis approximately through their centers), which are the mechanical fulcrum nearest to the canines and the point of application of motion from neck and body, (c) the approximate center of gravity, the motion of which is related to the general direction of momentum, and (d) the center of rotation. In distinction from Bohlin's analysis, it is again emphasized that the center of rotation is not necessarily a mechanical fulcrum or anatomical joint. It is an imaginary point helping to visualize and analyze complex motion derived from the joint action of a whole series of real fulcrums no one of which is likely to be quite stationary: all the joints of the axial skeleton, especially those of the neck, and also to some extent all the limb joints, especially those of the fore-limb. The center of rotation may be at almost any point within or outside of the animal.

Circumlocution can be avoided by a few simple definitions for present purposes. A pure stabbing motion means a stroke in and then out with a minimum of cutting consistent with the form of the weapon. Cutting is used in the ordinary sense, but for distinction the word slicing is used to mean cutting not necessary merely to insert and withdraw the weapon. Down-

slicing is such extra cutting performed during the insertion of the weapon and up-slicing during its withdrawal. Straight-

slicing is performed with the weapon remaining at approximately the same depth in the wound.

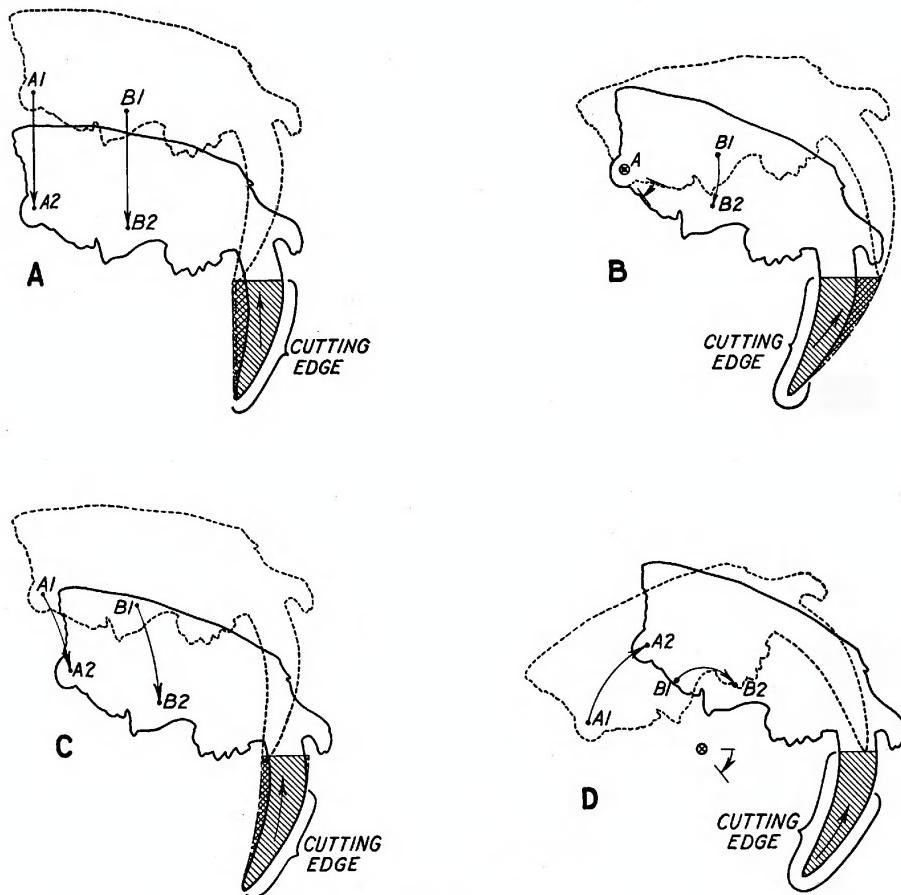


Fig. 1. Diagram of possible methods of stabbing in *Smilodon*. A, motion straight downward. B, rotation of skull on the condyles. C, rotation on the cervico-dorsal joint. D, rotation around the center of curvature of the canine axis. In all figures, two phases are shown, 1 at the beginning of insertion of the canines, and 2 at its completion. The skull is shown in broken outline in phase 1 and solid outline in phase 2. A is the condylar center of rotation and B the approximate center of gravity, and the affixed numbers show the positions of these points in each of the two phases. The circle and cross in B and D are centers of rotation. The arrow on the canine is the approximate direction of greatest strain. The simply cross-ruled area is the cutting necessary for insertion of the canine and double cross-hatching represents slicing, unnecessary for such insertion.

STABBING

The simplest stabbing motion would be straight down, Fig. 1A. This involves considerable slicing, which represents a loss of effort in pure stabbing; it puts great oblique strain on the delicate tip of the tooth; and it uses almost the whole of the

anterior edge and none of the posterior edge for cutting. It is obvious that the posterior edge is the more efficient for cutting and that the proximal part of the anterior edge is often incapable of cutting. It seems quite impossible that the animals

habitually stabbed in this way (which would, moreover, be a difficult motion to impart to the head with any force).

Rotation about the condyles, Fig. 1B, also involves some (but less) slicing. The stress is somewhat oblique, although probably not enough to cause unbearable strain. Cutting is mostly on the posterior edge, as it should be, with a little on the distal end of the anterior edge, which is also morphologically justified. Such stabbing was entirely possible, but Bohlin is clearly right in concluding that the anatomical structure is not perfectly adapted to it. Aside from the probably insignificant loss of cutting efficiency, the principal disadvantage is that power is derived only from the muscles depressing the head on the atlantal joint. These are powerful, but the loss of any help or momentum from post-cranial movement would be inefficient. It is incredible that the animals should have tended to hold the atlas quite motionless while moving the head violently.

Bohlin believes that stabbing motion would really be by rotation on the cervico-dorsal joint (Fig. 1C), and he concludes that the canines are ill-adapted for stabbing by such a motion. A small amount of slicing is involved. The stress on the tip is oblique, but only slightly and probably not dangerously. The serious disadvantages are that cutting is entirely on the anterior edge of the canine, and that little or no action by the head-depressing muscles is involved, although these are known to have been unusually powerful and can only be inferred to have been hypertrophied by functional relationship to the canines. I emphatically agree with Bohlin that the sabertooths did not habitually stab in this way, while disagreeing just as emphatically with his conclusion that they therefore did not stab at all.

Rotation about the center of a circle of which the axis of the canine is an arc, Fig. 1D, imparts a perfectly efficient pure stabbing motion to the canines. There is no slicing and the cutting incidental to pure stabbing uses the whole of the posterior and about two-thirds of the anterior edge of the canine. The proportion of the anterior edge involved in cutting with this motion

varies according to the shape of the tooth. In *Thylacosmilus*, for instance, only a small distal part of this edge would need to cut, while in some machairodonts almost the whole edge would be involved. It is not likely to be a coincidence that in each case the part of the anterior edge that must cut for greatest efficiency with this motion does in fact have a cutting edge while the more proximal, theoretically non-cutting part does not.

The relation of this motion to the musculature is also advantageous. The motion would result from a thrust of the head forward and its simultaneous depression. Although the occiput tends to rise somewhat, no lifting muscular effort is involved; this is a mechanical result of forward thrust against the occiput accompanied by strong depression of the head on the occipito-cervical joint. A forward lunge is the universal motion of attack, and one of which the sabertooths were certainly well capable. The depression of the head on its fulcrum is, as already noted, provided for by unusually strong muscular development in just these animals. Bohlin adduces as evidence against stabbing that the attacking sabertooth would have to come to a full stop before stabbing and then start a new motion at right angles to the momentum of attack. On the contrary, my analysis seems to show that the attack and the stab would follow naturally and that much of the attacking momentum would be utilized in driving in the sabers. Instead of being less, this seems to me a mode of attack decidedly more efficient than in the "normal" (non-sabertooth) carnivores, in which the forward momentum helps little or not at all to drive in the teeth.

Merriam and Stock (1932, p. 46) state that the canine curvature in *Smilodon* makes it "probable that the downward stroke of the tooth must have been accompanied by a backward jerk in order to make it fully effective." If by "backward jerk" a rotation of the head downward on the occipital condyles is meant, this agrees with the result reached in this paper, but it is to be emphasized that backward motion transmitted to the head from the neck would result mainly in slicing, as discussed

later. Merriam and Stock agree that these teeth are chiefly stabbing weapons, and pure stabbing demands that the motion transmitted to the head should not be backward.

This mode of stabbing theoretically requires that the center of the curvature of

have investigated, including several genera of machairodontines and the quite independently evolved sabertooth marsupial *Thylacosmilus*, this point is indeed in the region so delimited (Fig. 2). Within this region its exact position varies considerably, even by individual variation within

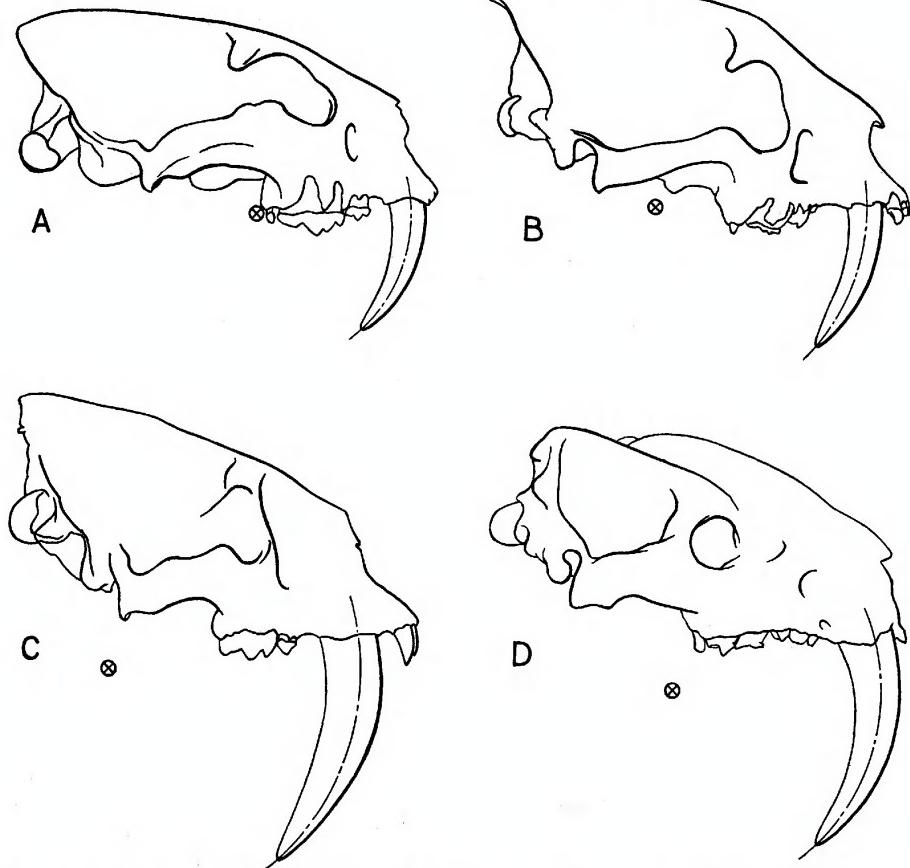


Fig. 2. Skulls of sabertoothed mammals, showing axes of the canines and the centers of curvature of these axes. A, *Machairodus*. B, *Hoplophoneus*. C, *Smilodon*. D, *Thylacosmilus*. Base for A from Filhol, for B from Matthew, for C from Merriam and Stock, and for D from Riggs. Not to scale.

the canine axis should be well above the canine tip (when the skull is oriented with the palate approximately horizontal), at or a short distance below the alveolar level, below and anterior to the condyles, and posterior to the canines by about half the distance to the occiput or somewhat more. In all the sabertoothed animals that I

one species. It is often modified by postmortem crushing, and it may also be subject to progressive phylogenetic adaptation—a point worthy of more detailed investigation. (Klauber finds that the fang curvature is a taxonomic character in snakes.) Canines with the center of curvature well posterior to the head, which Bohlin con-

siders theoretically necessary for efficient stabbing, would give little use to the head-depressors which are apparently the most important head muscles in all these animals. It thus seems that less curved canines would really be much less efficient stabbers than the canines that really occur. It is also significant that venomous snake fangs, which certainly are efficient stabbing weapons and the mechanics of which are analogous to those of saberteeth without being

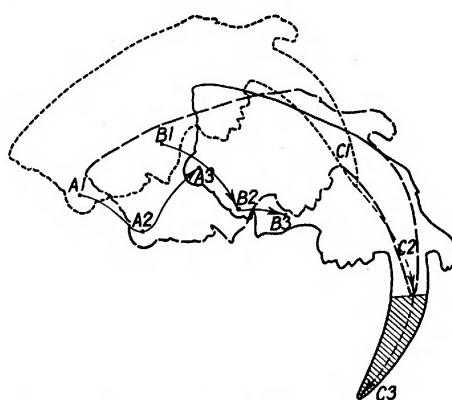


Fig. 3. Diagram of last phases of attack by *Smilodon*. Phase 1, approach, with skull in dotted outline; 2, beginning of stab, broken outline; 3, end of stab, solid outline. A, center of condyle. B, approximate center of gravity. C, end of canine. Ruled area is that cut by penetration of canine.

exactly the same, have the center of curvature in a region mechanically analogous to that found in these mammals.

In short, I believe that stabbing in this way is the action for which the whole saber-tooth structure is most efficiently adapted. Doubtless the completely perfect stab of

the diagram was as rare as perfection always is in nature, but this seems to be the true norm and the adaptive goal of this type of structure.

The more extended final phases of such an idealized normal attack, subject to the myriad deviations of circumstances, are diagrammatically represented in Fig. 3. Here motion from 1 to 2 is the final phase of approach in the attack and phase 2-3 the stabbing thrust of the canines. In phase 1-2 the body is moving forward, the neck and head whipping downward and forward. The head is rotating slowly but with increasing acceleration. At 2 the canines hit the prey and a pivoting motion begins—the sudden encountering of resistance on this fulcrum would itself tend to initiate and to assist the pivoting (as would also the contact of the open lower jaw). Forward and downward motion of the head as a whole continues, modified by the still greater acceleration and snapping contraction of the head-depressors as the canines are driven in along their axes. The head might be said to rock forward on the canines, and so transmits in this new direction the greater part of the momentum of the approach.

As far as I know, the only direct evidence of use of a canine saber is that described by Scott and Jepsen (1936, p. 148), a skull of *Nimravus* with a wound exactly such as would be produced by pure stabbing motion by the associated saber-tooth *Eusmilus*. One example does not necessarily indicate a habit, but it does prove a possibility. Incidentally this wound was inflicted on a living animal and not on carrion, a point to be discussed later.

SLICING

Consideration should also be given to the possibility of purposeful slicing, as opposed to slicing incidental to deviations from perfect stabbing. Most adherents of the stabbing theory have considered slicing as a probable accompaniment or secondary function. Bohlin considers it the primary function. In the first place, slicing without stabbing seems unlikely. The canines cannot slice unless they are inserted in the

hide or flesh, and the easy way to get them in would be by stabbing, whether in its pure attack form or in some modified manner.

Straight slicing considered as an activity independent of stabbing is diagrammatically shown in Fig. 4A. Personal experience of the practical impossibility of cutting tender meat with a sharp knife without hacking or sawing motion is suggestive of the tremendous effort necessary for a

sabertooth to slice tough hide and muscle in this way with its duller weapon. In view of the very oblique strain involved, it is doubtful whether the teeth could stand continual application of this great force even if the animal could exert it.

(Fig. 4B), up-slicing (Fig. 4C), or both (Fig. 4D). In all three figures the amount of slicing is roughly the same. In down-slicing the head is jerked backward while being rotated (or depressed) about a center near or above the top of the posterior part

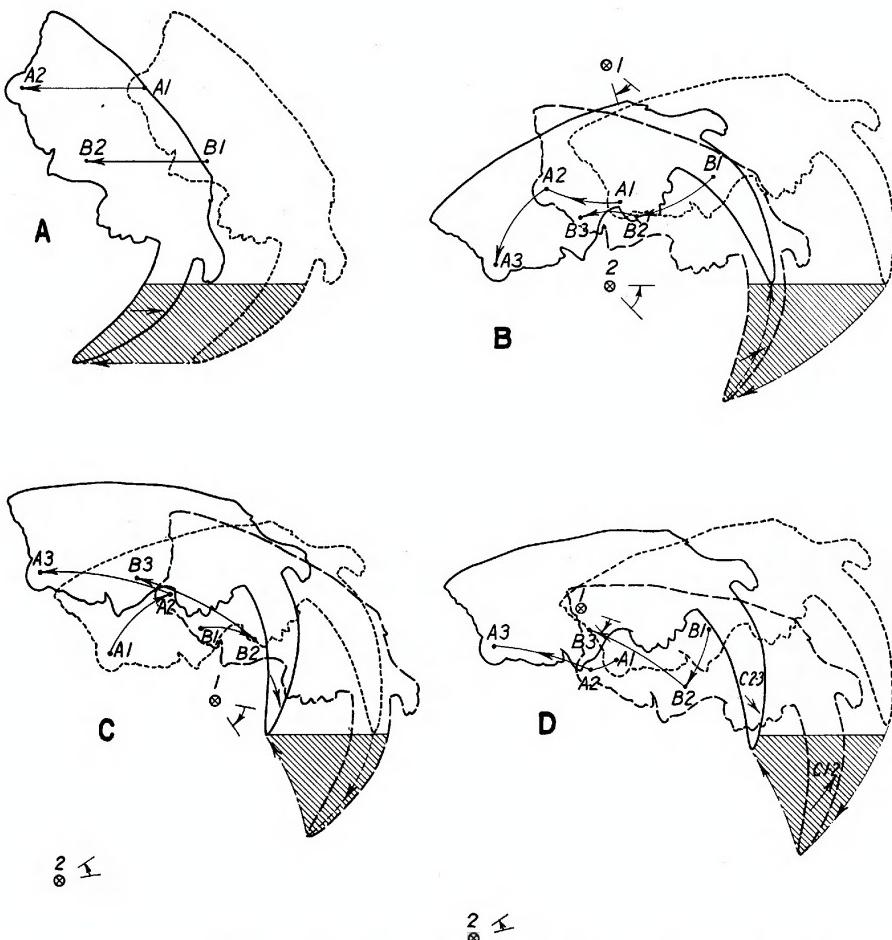


Fig. 4. Diagrams of slicing in *Smilodon*. A, straight slicing. B, down-slicing. C, up-slicing. D, down-and-up-slicing. Symbolism and construction of diagrams as in Figs. 1 and 3, except that whole cut is shown as a unit without distinction of slicing from cutting necessary for insertion of canine. The arrows on the canines represent approximate direction of greatest stress in the phase immediately preceding the given position of the canine.

It seems probable that a sabertooth with the desire or necessity of slicing with the sabers would adopt the expedient of hacking, that is, of combining stabbing and slicing (a straight chopping motion against the edge being out of the question). Such stab-slicing could involve down-slicing

of the skull. The saber is then withdrawn without cutting by rotation in the opposite direction around the center of curvature of the canine. The oblique strain, especially on the tip of the canine near the beginning of the cut, would be great. If a slice of any considerable extent were made at one stroke

the direction of motion would tend to be nearly at right angles to the cutting edge, minimizing shearing or sawing action and making the cutting very difficult.

In up-slicing the canine is first stabbed in by pure stabbing without slicing and is then withdrawn by pulling the head backward and upward, or with rotation about a point below and behind the center of canine curvature. (In such a case a diagram showing rotation on a fixed point is doubtless over-simplified; the center of rotation probably moved and the true course might be more nearly a section of a spiral than an arc of a circle.) This would probably require somewhat less effort than down-slicing, because the difficult insertion is accomplished in the easiest possible way and the cutting could largely be performed by rocking backward on the fore-limbs against the gradually decreasing pull of the head-depressors. The effort would nevertheless be great and a long slice would require almost prohibitive exertion and transverse strain on the tip of the canine.

A down-and-up slice can be accomplished by relatively straight backward motion at the condyle, accompanied by depression and raising of the head, mechanically equivalent approximately to rotation first about a point near the posterodorsal end of the skull and then rotation in an opposite direction about a point below the posterior end of the skull. This second rotation would follow almost automatically from the backward pull against the cutting resistance. Such motion is smoother and easier than either pure down- or up-slicing, and it seems psychologically and physically a more natural motion for an animal to make. For a given size of slice, its efficiency would also be greater because the angle of the cutting edge to its work would be more acute, increasing the relatively easy sawing or shearing component, and its safety would be greater because less (although still considerable) strain would be put on the tip of the tooth. On the whole it seems probable that if the animal did intentionally slice, it would tend to do so in this way.

The result of such an action is somewhat like that of a stab that is unnecessarily

broad. As typically developed, however, the down-and-up slice is unlike the pure stab. In the former the neck or body motion is backward, in the latter predominantly forward. One would be used more on disabled or dead prey, the other more in attack on active prey. A sabertooth in action would not be concerned with following diagrams or maintaining maximum efficiency, and undoubtedly would use all sorts of variant and intermediate motions, but pure stabbing and down-and-up slicing seem to be the norms of the two most likely uses of the canines.

Another factor to be considered is the possible effect of preponderance of strain at the alveolus in any one direction other than along the tooth axis. It is well known that such pressure has a tendency to make the alveolus move. Thus under normal conditions the alveolar, and hence also the coronal, orientation may often be inferred to be one such that the tooth axis represents the average direction of pressure. In any sort of stabbing except that shown in Fig. 1D, the average pressure is not along the tooth axis. Pure stabbing as in Fig. 1D is the only likely action that centers strain in the direction of that axis, and therefore is probably the normal use correlated with the observed orientation. Any probable sort of slicing is almost certain to produce a pressure component tending to rotate the crown forward about the aveolar mouth as a fulcrum or to move the alveolus itself forward. For a given amount of slashing, this component would probably be weakest or least constant in down-and-up slicing as in Fig. 4D. It is improbable that the observed orientation was developed in relation to slicing of any sort as the predominant use of the teeth, although probable that a moderate amount of slicing as a secondary activity would not seriously disturb the orientation correlated with stabbing. Other factors enter into the situation (such as a growth or other tissue pressure counteracting the pressure of use) and some animals do habitually use teeth with pressure oblique to their axis and predominantly in one direction. The argument cannot, in itself, be considered conclusive, but it is at least suggestive.

GENERAL HABITUS

If it be granted that sabertooths could and sometimes did slash as well as stab, the question remains whether the sabers are primarily an adaptation to one or to the other. It may be misleading to speak of primary or principal adaptation to one function among several. An organ that is used in more than one way has a function that is multiple but that it fulfills as a unit. Nevertheless one use or function may fairly be called principal and primary if it had greater selective value or in any other way was more particularly concerned with the radical structural divergence of one group from another, in this case of the sabertooth from the "normal" flesh-eaters, the machairodontines from the felines or the thylacosmilines from the borhyaenines.

Fully developed or pure slicing with sabers would, as Bohlin concludes, be useful principally for dismembering dead prey or carrion. Now such slashing does not seem to me to be an advantageous way of accomplishing this end. Lions, hyaenas, and other carnivores with "normal" canines certainly accomplish this work adequately for their own needs, using the carnassials for slicing and the canines and incisors for holding and tearing. Indeed if there is any selective value in this function, it may well favor "normal" canines—possibly this is a factor in the development of feline canines if, as Matthew believed on the basis of strong evidence, they evolved from canines intermediate between the specialized feline and machairodontine types. The considerations already expressed suggest that the sabers are not really well adapted to tearing out long strips of flesh, the one way in which some real advantage over the felines in slicing seems possible. It would beg the question to say that the ability to pierce thicker skin on carrion was the fundamental difference, because the more efficient way to pierce such skin, whether on a live or a dead animal, is by stabbing, not slicing.

The one thing that a saber can do efficiently, for which it surely serves well and for which no part of the feline dentition serves well or at all, is stabbing. I therefore conclude that stabbing was in some sense, not necessarily causative, primarily

correlated with the differentiation of the saber canines from "normal" canines and therefore that it is the principal functional element in the sabertooth specialization. If, as they undoubtedly did, the sabertoothed mammals also used the sabers to some extent for slashing and dismembering the prey, this was because they had sabers and necessarily used them as best they could, not because the sabers are the best way to serve this need and were developed in relation with it.

A few additional objections to the stabbing theory may be more briefly considered. A few students, especially Abel (e.g., 1939 and several earlier comments), deny that the mouth could be opened wide enough to stab in this way. Among others, Matthew (1910) and Bohlin (1940) have sufficiently exposed the complete fallacy of this objection. Perhaps a conclusive point is that if the argument were logically applied to some sabertoothed animals other than *Smilodon*, it would lead to the conclusion that they could not have fed themselves at all.

In the diagrams of this paper the lower jaw is omitted for clarity, but similar experiments were made with the jaw included and it was found that the activities here considered normal for sabertooths were not impeded and may well have been assisted by the mandible. (Klauber shows that the mandible assists in insertion of rattlesnake fangs, and analogous action is quite possible in sabertoothed mammals.)

Bohlin's objection that a sabertooth must have performed the difficult action of attaching itself to its live prey before stabbing depends largely on what I believe to be his mistaken view as to the motions involved in stabbing. The animal did not have to come to a full stop before it started the stabbing motion. On the contrary, forward attack was a useful preliminary phase of stabbing and contact with the animal coincided with the strongest stabbing momentum. If attachment were subsequently needed, the insertion of the teeth is itself an attachment: dogs normally and cats frequently hold their prey in this way. It is also incredible to me that machairodonts could not cling to the back of an animal with their powerful limbs and pre-

hensile claws as do lions. Schaub (1925), especially, has concluded that machairodont fore-limbs were even better adapted for grasping prey than are those of felines.

Bohlin's further comment on the relatively weak hind-limbs relates more to the question of predaceous as against carrion-eating habits, but here, too, the conclusion does not necessarily follow. Machairodontine hind-limbs are very powerful: the misconception that they are weak arises from the relatively still greater development of the enormously strong front limbs. Merriam and Stock (1932, p. 25) point out that in *Smilodon* the hind-limbs are comparable in size (and also in strength) to those of the large living felines and, far from supposing that leaping was unlikely, these best informed of authorities on smilodont anatomy conclude that there are special adaptations for leaping or lunging at prey. Among the older machairodontines such as *Hoplophoneus*, it is also noticeable that the hind-limbs are as strong as those of comparable felines but that the fore-limbs are stronger. Although not adapted for swift running, the machairodont limbs seem fully consistent with hunting by stalking and ambush followed by a short, leaping or lunging attack perhaps balanced and powered in considerable degree by the front legs.

These front legs would themselves be powerful weapons and they could have served—as sometimes do the weaker front limbs of lions—to deliver the coup de grace to an animal slowed or stopped by the canine stab. Thus the unusually powerful fore-limbs and the unusually long canines might possibly be considered as coöordinated parts of a dual apparatus for killing prey.

Among living mammals, the closest analogy to the carnivore sabers is found among the hornless ruminants, *Moschus*, *Tragulus*, and their allies. With these can be associated some extinct forms like *Blastomeryx* and related genera. I have not found a detailed description of the exact mode of use of the tusks in the living forms, although several authors speak of the males as hacking or striking downward with the head. The canines do not reach the enormous proportions of the carnivore sabers, nor

do they entirely prevent biting action. The great specialization of neck and jaw muscles and of the jaw articulation seen in the sabertooth carnivores is lacking in these ruminants. The tusks are curved and in some if not all cases the center of curvature is in about the same region as in the carnivores and does not coincide with a joint. For what the analogy is worth, the most important point is that these most nearly analogous weapons of still living animals are used entirely for offensive attack. The purpose of disabling or killing is the same whether in order to eliminate a sexual rival or to obtain food. The ruminant canines obviously were not evolved in relation to tearing strips of flesh from carrion.

Another possible analogy is provided by the extinct uintatheres, but its value is lessened by the fact that the use of the canines in these animals is itself only an inference, based largely on the living tusked ruminants, which are more like the uintatheres in this respect than are the sabertoothed carnivores. The canine curvature is highly variable but tends to follow the principles already sketched and the action seems to have been a downward hook or stab. Here, again, the purpose was surely offensive attack on living rivals.

The tusks of swine and of some extinct forms like the astrapotheres are so unlike the sabers here under discussion as to provide little basis for inference. The only point worth mentioning is that in addition to rooting for food (an action for which the sabers certainly were not used), the tusks of swine are used offensively and that the action is to impale the enemy by a rotary movement more or less along the axis of the tooth—necessarily a very different motion from that of the sabertooths, but impaling has some slight analogy with stabbing. Other animals with enlarged anterior teeth, like the proboscideans and the rodents, are too dissimilar to provide any useful comparison.

The snake analogy, already briefly considered in the extent that seems valid, involves the mechanics of tooth insertion and cannot well be extended to inferences as to general habitus. The snake fangs are obviously adapted for attack on living ani-

mals, but the fangs as such do little injury and the vital point of the attack is the injection of venom. The predaceous habits of snakes therefore do not particularly reinforce the inference that sabertoothed carnivores were predaceous.

One difficulty in the stabbing-predator theory is that it must frequently have happened that the canines failed to pierce a vital spot and that bleeding, as suggested especially by Matthew, might be slow to disable a large animal. This difficulty does not exclude predaceous habits, which do not require that all attacks result in immediate death of the prey, and it is largely removed if the fore-limbs were used as a second weapon.

Few carnivores refuse carrion and the question again is whether this action was primary or secondary as regards the saber-tooth specialization. The evidence seems to me decidedly to favor the usual view that these animals were primarily predators. Bohlin's suggestion that animals with broken sabers came to depend on carrion seems very probable, but it is beside the point in considering the functions of the canines when these were present.

A final objection, also by Bohlin, is that the presence of two canines, rather than one, more than doubled the difficulty of stabbing. It must be remembered that snakes strike very successfully with two fangs. It would be genetically improbable that one canine, alone, could develop as a saber, since it appears to be the rule (with sundry exceptions) that symmetrical structures are governed by one set of genes, not by two independent sets. The develop-

ment of a single saber would also require very complex compensatory adjustments throughout head and neck. If the presence of two sabers were less advantageous than one, the question would be whether this disadvantage outweighed the selection value of stabbing. It is reasonable to suppose that it did not. Nor is it clear that the presence of two sabers was really disadvantageous. They inflict twice as severe a wound, cause twice as much bleeding, and have twice as much chance of finding a vital spot. The strength to drive two sabers into the prey certainly was present. On the other hand, slicing requires more effort than stabbing and objections that two canines are disadvantageous might apply with still greater force to the slicing theory. It is, indeed, possible that slicing would involve less danger of snagging the canines or breaking one against a bone. As regards breakage by stabbing, the presence of two canines is advantageous because it cuts in half the chances of total loss of these weapons—note, among others, the South American *Smilodon* in the American Museum that continued the use of one saber after the other was lost. The further precaution of continuous replacement, as in snakes, would have been still more advantageous, but the materials for evolution in this direction were probably lacking: mutations in the direction of polyphyodontism seem to be extremely rare in mammals. The sabertooths did have well-developed and long-functioning deciduous canines, which is about as far in this direction as a mammal is likely to be able to go.

SUMMARY

1.—The sabertooth specialization has arisen independently at least three times among carnivorous mammals. Conflicting theories are that they were used for stabbing, for slicing, or for both, and that they were related to predaceous or to carrion-eating habits.

2.—Stabbing with a curved tooth involves rotary motion, the center of which is not normally at an anatomical joint. Contrary to the most recent study, that of Bohlin, the mammalian saberteeth and the associated osteological and myological specializations are perfectly adapted for stabbing.

3.—The known saber-like canines are ill-adapted for slicing, but doubtless could be and were used to make a short stabbing slice or gash. This function is considered secondary and the stabbing attack primary.

4.—This primary adaptation of the canines and the general bodily structure are more consistent with predaceous habits than with carrion-eating. The various objections to the predaceous-stabbing theory seem all to be based on misapprehensions or to permit equally logical alternative deductions.

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